Daily and Seasonal Activity Patterns of *Rhagoletis indifferens* (Diptera: Tephritidae) in Washington State

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ABSTRACT The diurnal and seasonal activity patterns of the western cherry fruit fly, *Rhagoletis indifferens* Curran, were determined on three sweet cherry trees, *Prunus avium* (L.), from 0700 to 1900 hours during June and July 2001 in Yakima County, WA. There were significant effects of time of day and season on numbers of flies seen on fruit relative to leaves, indicating that presence on or attraction to these substrates for feeding, mating, or oviposition, whether caused by visual or chemical cues, was greatly modified by temperature. When temperatures were 15–16°C at 0700 hours in early June, flies of both sexes were seen mostly on leaves, but when the temperature reached 20°C, more flies of both sexes moved onto fruit. Peak fly sightings occurred at 25–35°C, usually after 1000 hours. At >35°C, most flies vanished from view, and those seen were less active. Over the entire season, males were seen four times more often than females and spent more time on fruit than on leaves. Females were seen equally on and spent equal time on fruit and leaves when temperatures were 20–35°C. Mating was initiated on fruit but was completed on fruit and leaves. Overall fly sightings and daily temperatures were positively correlated early in the season when it was cooler, uncorrelated in the middle of the season, and negatively correlated in late season when it was warmest. The results show that *R. indifferens* presence and times spent on fruit and leaves are greatly altered by daily and seasonal changes in temperature, but they also suggest that at 20–35°C substrate-seeking behaviors of each sex do not change with time of day or season.

KEY WORDS *Rhagoletis indifferens*, daily and seasonal activity, mating, sweet cherry

THE GENERAL ACTIVITY patterns of flies in the genus *Rhagoletis* in nature have been well studied. General activities, feeding, and mating behaviors in the field have been documented for the apple maggot, *Rhagoletis pomonella* (Walsh) (Prokopy et al. 1972), the eastern cherry fruit fly, *Rhagoletis cingulata* (Loew) (Smith 1984), the black cherry fruit fly, *Rhagoletis fausta* (Osten Sacken) (Prokopy 1976), the blueberry maggot, *Rhagoletis mendax* Curran (Smith and Prokopy 1981), *Rhagoletis conversa* (Bréthes) (Frías et al. 1984), *Rhagoletis cornivora* Bush (Smith 1985a), *Rhagoletis tabellaria* (Fitch) (Smith 1985b), *Rhagoletis zephyria* Snow (Tracewski and Brunner 1987), *Rhagoletis turpiniae* Hernández, and *Rhagoletis zoqui* Bush (Aluja et al. 2001). The results from these studies indicate that activities and behaviors of *Rhagoletis* flies on different hosts share common features, most notably that males and females are usually seen more often on fruit than leaves. Presence on fruit or leaves may be influenced greatly by a fly's need to feed, mate, or lay eggs. It is generally assumed that leaves are the primary feeding sites (Prokopy 1968), whereas fruit are clearly egg-laying sites, although fruit are also sites for feeding (e.g., Frick et al. 1954, Smith 1984) and mating (Prokopy et al. 1971).

Despite the wealth of information on *Rhagoletis* spp., the activity patterns and behavioral characteristics of the western cherry fruit fly, *Rhagoletis indifferens* Curran, have not been determined in nature. *R. indifferens* is the major pest of sweet cherries, *Prunus avium* (L.), and sour or tart cherries, *Prunus cerasus* L., in the northwestern United States. Much is known about the basic biology of *R. indifferens* largely because of the comprehensive study by Frick et al. (1954).

In general, adults emerge from the ground in late May to June, continue to do so throughout harvest in mid- and late June, and stop emerging by around mid-July. Eggs are laid into fruit after a preovipositional period of 6–13 d. A single female can lay 386 eggs. The period from oviposition to larval emergence lasts 11–25 d, depending on temperature. Flies exit the fruit, drop into the soil, pupate, and enter diapause, emerging the following year. There is only one major generation a year, with a small second generation that does not undergo diapause. Based on last emergence to last bait trap catch data, adults live 15–30 d in nature (Frick et al. 1954).

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Observations of the activity patterns and behaviors of *R. indifferens* are consistent with those of other *Rhagoletis* spp. Flies were most active on warm days. On the hottest days, flies were most numerous on the north side of trees, but on cool days, flies were found on the sunny sides. Limited mating observations indicated that pairs remained together for several hours. In addition, flies were usually found clinging to the bottom or lower side of the fruit (Frick et al. 1954). These observations were not quantified, however, and no mention was made of the abundance of males and females on fruit versus leaves, the numbers seen mating during the day and over the season, and the relationships these numbers have with environmental factors such as temperature.

In this study, I documented the daily and seasonal changes in activity, the use of fruit and leaves by males and females, mating behaviors, and horizontal movement within trees of *R. indifferens*, with special reference to temperature effects. The main objectives were to better understand key ecological and behavioral characteristics of *R. indifferens*, to understand how these may be adaptive, and to compare findings with those of other *Rhagoletis* spp.

Materials and Methods

Study Trees. Three 6–9 m tall, 8–10 m diam 'Bing' sweet cherry trees in residential yards in Yakima County, WA, were used to observe *R. indifferens* activity during June through July 2001. Trees supported heavy fruit loads and had been identified as infested by placing yellow Pherocon AM traps (Trécé, Salinas, CA) in them in mid-May. Trees 1 and 2 were located in the city of Zillah. Tree 1 was isolated in a yard without other cherry trees within 100 m. Tree 2 (5 km from tree 1) was located in a yard with three adjacent and similar-sized cherry trees. Tree 3 (20–35 km from trees 1 and 2) was located in the city of Yakima and was isolated in a yard without other cherry trees. Based on trap catches, first fly emergence from under trees 1, 2, and 3 occurred around 19–23 May, 24–28 May, and 1 June, respectively. Based on cherry fruit size and ripeness, trees 1 and 2 had similar phenology. Fruit on both were fully ripe (dark purple, nearly black) 2 wk before those on tree 3. On 6 July, additional observations were made on a 7-m tall, 8-m diam sour cherry (tree 4), in Yakima.

On two dates in July and August, six additional sweet cherry trees (trees 5–10) were used in an activity duration study. Trees were located in backyard lots in the cities of Cle Elum and Roslyn in Kittitas County (where fruit development is slower than in Zillah and Yakima); they were 3–7 m tall and 2–10 m in diam and were heavily loaded with fruit.

Recordings of Activity. Recordings of types and locations of fly behaviors in tree 1 (4, 13, 20 June and 1, 12 July), tree 2 (6, 16, 21 June and 3, 11 July), tree 3 (9, 17, 22 June and 4, 10, 17 July), and tree 4 (6 July) were made for 12 h from 0700 to 1900 hours on sunny or partly sunny days. Recordings were made until most or all of the fruit dropped, and adult flies disappeared. Each tree was inspected for a 20-min period each hour. Consecutive 5-min searches were conducted in each of the east, south, west, and north quadrants. Each quadrant was about 3–5 m along the tree periphery and covered ≈50–60 m^2 of the lower tree canopy. Locations within each quadrant were inspected only once per 5 min to prevent counting the same flies. Flies were carefully approached and were not disturbed while being observed. To eliminate observer bias, the two observers in the study worked alongside one another and checked each other's recordings to ensure they were in agreement. A total of 68 h of direct observations was made during the study. Fly activities up to 3 m above ground were recorded. A stepladder was used to access higher tree levels for inspection. Temperatures in each of the quadrants were measured using a thermometer probe hung from a middle branch. On three representative days, light intensity was also measured outside the canopy in each of the quadrants over 12 h using a pyranometer (Li-Cor, Lincoln, NE).

Recorded fly behaviors were numbers of males, females, and mating pairs on fruit, leaves (lower and upper surfaces), and branches; male "boxing behavior," in which males fight each other using their prothoracic legs (AliNiazee 1974, Messina and Subler 1995); female ovipositor probing on fruit; and feeding on visible food (bird feces and fruit juice). These behaviors reveal the flies' use of different substrates for feeding, mating, or oviposition, and consequently were important in explaining and describing fly activity patterns and how they may affect trapping and management efforts. Foraging behavior on leaf surfaces (with proboscis contact) was not consistently recorded because it was too difficult to define or to see when flies were sighted from below.

Activity Duration. In addition to recording types and locations of fly behaviors in trees, the duration of apparent resting or waiting behaviors on fruit and leaves, mating, and boxing behaviors was determined on a few dates. Male and female flies were observed as they landed on leaves or fruit; the total times that flies spent there were recorded. On five dates during June through July 2001, recordings were made on trees 1–3 between 1100–1530 hours. On four dates in July, mating duration on fruit and leaves as well as boxing duration were recorded on tree 3 only. On 30 July and 6 August, total stay and mating duration on fruit and leaves on trees 5–10 were also recorded between 0930–1200 and 1230–1430 hours. Temperatures were recorded in the shade 1–3 m from locations of observations.

Statistical Analyses. Analyses were conducted to determine daily and seasonal differences in the numbers of flies on leaves and fruit, mating activity, horizontal movement, and other factors for trees 1–3. Data were analyzed within weeks (daily activity) and over weeks (seasonal activity). Repeated-measures analysis of variance (ANOVA) was conducted, with the experimental units (subjects) being the three populations of flies in the three trees in all cases. Time (hours within days or weeks during the season) was the within-subject quantitative effect, with different measurements on the same fly populations at different times. Three classes or explanatory variables were analyzed—substrate type (leaves or fruit), sex, and tree quadrant. The dependent variable was percentage of flies observed in these classes. A mixed, type 3 model, with tree (fly population) considered random and the other variables considered fixed (Winer et al. 1991), was used. Correlations between mean fly numbers and mean hourly temperatures within weeks were also calculated. Overall percentages of flies on fruit versus leaves (n = three replicates) and times spent on leaves and fruit over the season were analyzed with one-way ANOVA followed by Duncan's multiple range test. Randomized block ANOVA, blocking on date, was also conducted to determine date and substrate effects on times spent on leaves and fruit. Percentages were arcsine-transformed before analyses. All analyses were conducted using SAS version 8.0 (SAS Institute 2001). Means ± SE are reported.

Results

Daily Activity Patterns and Temperatures. There were significant effects of time of day on numbers of *R. indifferens* and percentage of males and females on fruit relative to leaves early in the season, but less frequently later (Fig. 1; Table 1), indicating that presence on or attraction to these substrates during the day, whether caused by visual or chemical cues, was greatly modified by temperature. When temperatures were 15–16°C at 0700 hours in early June (Fig. 1A and 1B), most male and female flies were seen on leaves. When temperatures increased to >20°C, more flies moved onto fruit. Flies left fruit and leaves by 1900 hours, when it was <20°C (Fig. 1A). Later in the season, when temperatures were 23–25°C by 0700 hours (Fig. 1C and 1 D), most flies were already seen on fruit, resulting in few time effects (Table 1). Peak fly sightings occurred at 25–35°C, usually after 1000 hours. At or above 35°C, there were few sightings (Fig. 1D and 1E). At 36–41°C (tree 3), most flies vanished from view, despite searches for flies in the interior of the tree, on the trunk, branches, and surrounding coniferous bushes. Flies reappeared after temperatures dropped below 36°C.

Seasonal Activity Patterns and Temperatures. Numbers of flies were highest during 4–22 June (Fig. 1 A–C), lower during 1–4 July (Fig. 1D), and lowest during 10–12 July (Fig. 1E), concomitant with higher daily temperatures and fruit drop, except in tree 3 (Fig. 1 F). The results show that fly activities and movement change during the season and that temperatures likely are a key factor affecting this change. However, numbers of flies on fruit relative to leaves and male-to-female sightings did not change during the season. Over the season, males were seen overwhelmingly more often on fruit (85.2 ± 2.3%) than leaves (14.8 ± 2.3%) (F = 291.68, df = 1, 4, $P < 0.0001$) (Fig. 1). There was a significant substrate effect (F = 326.05, df = 1, 25, $P < 0.0001$) on male sightings, but no seasonal effect ($P > 0.05$) on percentage of male sightings on fruit. Females were seen on fruit (50.6 ± 3.0%) and leaves (49.4 ± 3.0%) equally ($P > 0.05$) (Fig. 1). There was no substrate effect on female sightings or seasonal effect on percentage of female sightings on fruit ($P > 0.05$). When on leaves, females were seen more frequently on undersides (44.0 ± 7.6%) than males (23.8 ± 3.5%) ($P = 0.0686$). Almost no flies were seen on branches. Males (80.2%) were seen four times more often than were females (19.8%).

The correlation between overall fly sightings and daily temperatures depended on temperature ranges. Overall fly sightings and daily temperatures were positively correlated ($r = 0.754$, $P < 0.01$, to $r = 0.160$, $P > 0.05$) early in the season, 4–17 June, when it was 21.4–22.2°C (mean temperature during the day); uncorrelated in the middle of the season ($r = 0.276$, $P > 0.05$), 20–22 June, when it was 29.8°C; and negatively correlated ($r = -0.649$, $P < 0.05$, to -0.533, $P > 0.05$) in late season, 1–12 July, when it was 30.9–31.7°C

Duration Spent on Sweet Cherry Fruit and Leaves. Males spent significantly more time on fruit than leaves between 1100 and 1530 hours over the season (Table 2). Females spent equal times on leaves and fruit and the same time as males on leaves (Table 2). Females on fruit were more active than males on fruit, engaging in rapid walking and searching behavior. When temperatures were 36–41°C (9–10 July), flies became less active and time spent on both substrates by the few flies seen increased accordingly (Table 2).

Mating Activity. There was no effect of time of day on numbers of flies seen mating ($P > 0.05$), except during 13–17 June when more were seen in the afternoon ($P < 0.05$) (Fig. 2B). Daily and seasonal mating patterns on fruit and leaves (Fig. 2) reflected those of general fly sightings. Over the season, mating was seen equally on leaves (56.6 ± 3.7%) and fruit (43.4 ± 3.7%) ($P > 0.05$). Only two pairs were seen mating on twigs. Mating peaked during 20–22 June, when temperatures were 24–30°C (Fig. 2C). Few matings were seen at higher temperatures (Fig. 2D and 2E). Means of 5.9% males and 24.3% females, were seen mating over the season.

Initiation of fly mating was observed for a total of six pairs. Mating was initiated on fruit in all cases. Four of these matings were observed to completion. In the other two, the mating pair either flew away, or mating was disrupted by a second male. In two cases (13 and 16 July), the mating pairs flew to leaves, where mating was completed. The pairs spent 16.28 and 2.52 min on the fruit and 7.53 min and 42.68 min on leaves, respectively. In the other two cases (18 July), mating began and ended on fruit, lasting 28.27 and 34.12 min. When timed in progress (initiation not seen), pairs on leaves mated for 13.67 ± 3.40 min (n = 27), and pairs on fruit mated for 10.89 ± 2.90 min (n = 47) ($P > 0.05$). On leaves, 34.7% of pairs were seen mating on the undersides. Males also mounted other males on fruit in what appeared to be mating attempts.

Boxing Behavior. Only 0.7% of males on fruit engaged in boxing behavior during the season. However, on tree 3 on 17 July, 39.8% of males on fruit were seen

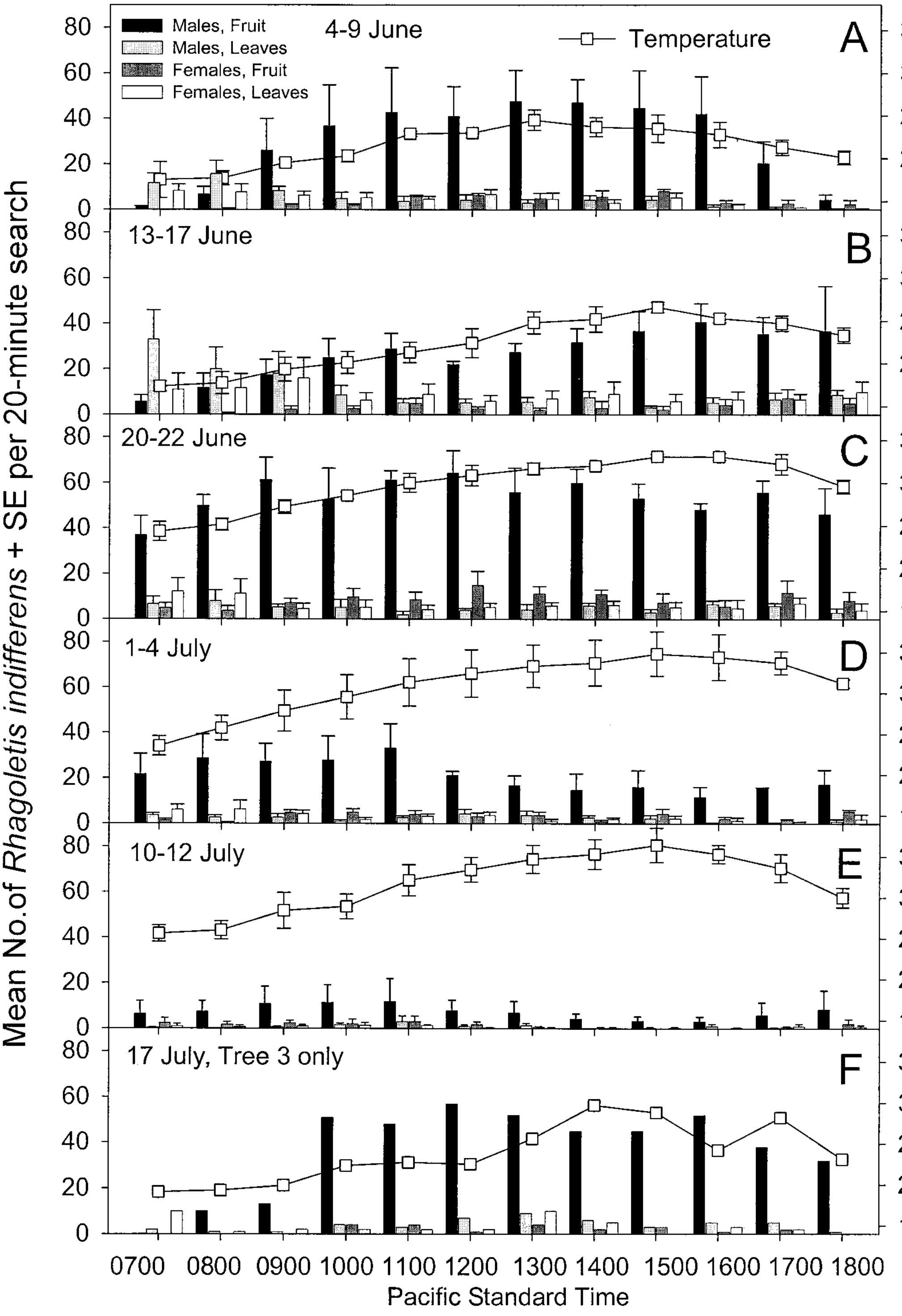

Fig. 1. Mean numbers ± SE of male and female *Rhagoletis indifferens* seen on fruit and leaves of three sweet cherry trees over 12 h during (A) 4–9 June, (B) 13–17 June, (C) 20–22 June, (D) 1–4 July, and (E) 10–12 July 2001, and on (F) one sweet cherry tree on 17 July 2001 related to mean temperatures (from four tree quadrants) in Zillah and Yakima, WA.

Table 1. Effects of time of day (0700–1900 hours) on percentages of *Rhagoletis indifferens* males and females seen on cherry fruit in 2001 in Yakima County, WA

Week	Males		Females	
	F	*P*	*F*	*P*
1) 4–9 June	11.50	**	20.09	***
2) 13–17 June	19.32	***	1.35	NS
3) 20–22 June	0.86	NS	0.00	NS
4) 1–4 July	1.52	NS	5.53	*
5) 10–12 July	5.68	*	1.10	NS

N = three trees (repeated measures analysis of variance, df = 1, 32).
***, $P < 0.0001$; **, $P < 0.01$; *, $P < 0.05$; NS, not significant ($P > 0.05$).

boxing between 0900 and 1600 hours. Because of high fruit removal by birds in this tree, male flies were forced to move onto the relatively few fruit at the lower heights. This may have forced males to occupy the same fruit, increasing the numbers of aggressive encounters between them. Boxing averaged 0.50 ± 0.08 min ($n = 64$) in duration.

Other Activities. Of all females observed, 7.6% were seen probing or ovipositing into fruit, and 0.92% were seen puncturing fruit and then feeding on the exuded juice, feeding on juice splattered on leaves (from bird feeding), or feeding on bird feces. Only 0.04% of males were seen feeding on fruit damaged by birds or from larval exit or respiration holes in fruit. Despite careful observations, no flies were seen feeding on extrafloral nectaries or on the honeydew of black cherry aphid, *Myzus cerasi* (F.), which was abundant on lower leaves of tree 3.

Daily and Seasonal Horizontal Movement Within Trees. Significant changes in fly presence among most quadrants within days during 4–9 June (F = 12.70–58.31, df = 1, 32, $P < 0.01$) (Fig. 3A) and 13–17 June (F = 76.26–87.92, df = 1, 32, $P < 0.0001$) were detected but generally not during other weeks ($P > 0.05$) (Fig. 3B). The changes were significantly correlated with temperatures among quadrants ($P < 0.05$) (Fig. 3C and 3D). Early in the season, most flies in the morning were seen on the east sides of trees, where it was sunny and >20°C, with almost none seen on the west sides, where it was shady and <20°C (Fig. 3A and 3C). Later in the day, flies moved to the south and the west sides. Later in the season, when it was warmer, flies were more evenly distributed among quadrants earlier in the day (Fig. 3 B and 3D). Numbers on north sides were relatively uniform throughout the day during the entire season. On the warmest days, 3 and 4 July, fly sightings were negatively correlated ($r = -0.686$, $P < 0.05$) or were not correlated ($P > 0.05$) with light intensity.

Daily Activity on Sour Cherry. The diurnal activity patterns on the sour cherry tree (Fig. 4) were essentially the same as those on the three sweet cherry trees. More males than females were seen, males were sighted more often on fruit than leaves, females were sighted equally on fruit and leaves (Fig. 4A), and mating was seen throughout the day (Fig. 4B). Horizontal movement (Fig. 4C) was similar to that seen on sweet cherry trees. Fly sightings were positively correlated with light intensity in east ($r = 0.734$) and west ($r = 0.732$) quadrants ($P < 0.01$).

Discussion

Temperatures were correlated with and were almost certainly a cause of changes in the daily activity patterns of *R. indifferens*, perhaps overriding the effects of visual or chemical cues used to find fruit or leaves for feeding, mating, or oviposition. Flies moved from leaves onto fruit as temperatures in the morning gradually increased, indicating the flies spent the night and early hours before sunrise off the fruit when temperatures were <15°C. Similar behavior was also

Table 2. Mean time (min) ± SE spent by male and female *R. indifferens* on individual sweet cherry leaves and individual cherry fruit or fruit clusters per visit from 1100–1530 hours (trees 1–3) and 0930–1430 hours (trees 5–10), 2001, in Yakima and Kittitas Counties, WA

Date	Tree[a]	°C	Males				Females			
			Leaves	No.	Fruit	No.	Leaves	No.	Fruit	No.
19 June	1	29–30	0.047 ± 0.003b	16	6.27 ± 0.50a	24	0.20 ± 0.02b	10	1.47 ± 0.18ab	14
2 July	2	30–32	0.03 ± 0.02a	2	4.63 ± 2.42a	10	—	—	1.43 ± 0.57a	7
9–10 July	3	36–41	7.97 ± 3.68a	21	9.40 ± 4.52a	11	13.48 ± 7.02a	10	0.63 ± 0.35a	7
13 July	3	32–36	0.07 ± 0.02b	21	5.35 ± 1.53a	37	1.50 ± 0.52ab	14	1.27 ± 0.33ab	14
30 July (0930–1200 hours)	5, 6	21–25	2.73 ± 2.22a	2	13.15 ± 3.87[b]a	21	—	—	—	—
30 July (1230–1430 hours)	7–10	21–24	0.60 ± 0.13a	14	4.03 ± 1.07a	31	1.59 ± 0.36a	17	5.11 ± 3.98a	9
6 August (0930–1200 hours)	7–10	24–28	0.63 ± 0.53a	6	4.72 ± 1.39a	46	0.95 ± 0.25a	20	1.52 ± 0.61a	15
6 August (1230–1430 hours)	7–10	28–31	0.58 ± 0.46a	4	1.97 ± 1.13a	19	1.79 ± 1.46a	7	1.70 ± 0.34a	22
Overall means			1.58 ± 0.96a		6.19 ± 1.24b		3.25 ± 2.06a		1.88 ± 0.55a	

Means followed by different letters within rows are significantly different (Duncan's multiple range test, $P < 0.05$).
[a] Trees 1 and 2, Zillah; tree 3, Yakima; trees 5 and 6, Cle Elum; trees 7–10, Roslyn.
[b] Seen in progress, not from initiation.

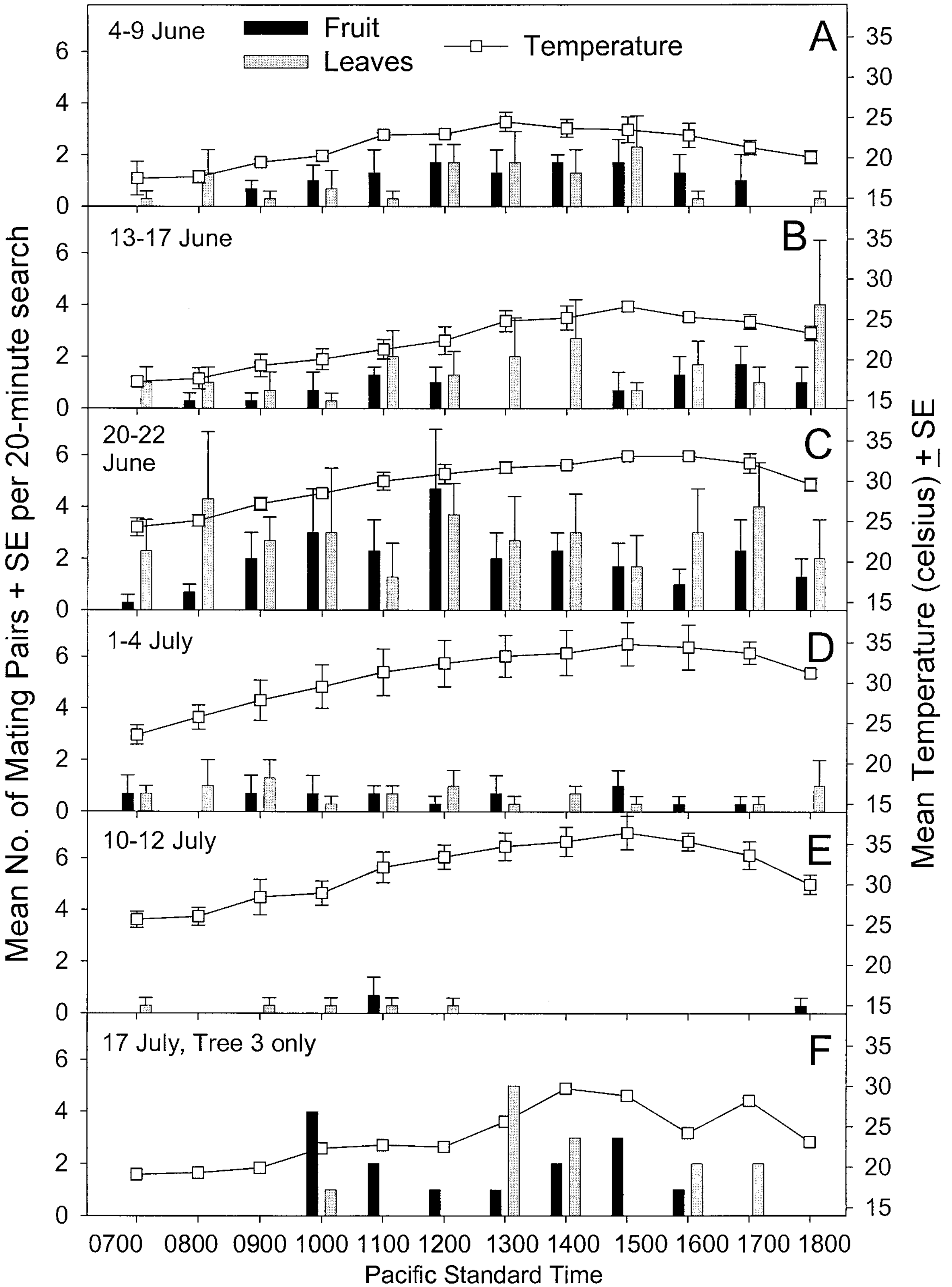

Fig. 2. Mean numbers ± SE of mating pairs of *R. indifferens* seen on fruit and leaves of three sweet cherry trees over 12 h during (A) 4–9 June, (B) 13–17 June, (C) 20–22 June, (D) 1–4 July, and (E) 10–12 July 2001, and of (F) one sweet cherry tree on 17 July 2001 related to mean temperatures (from four tree quadrants) in Zillah and Yakima, WA.

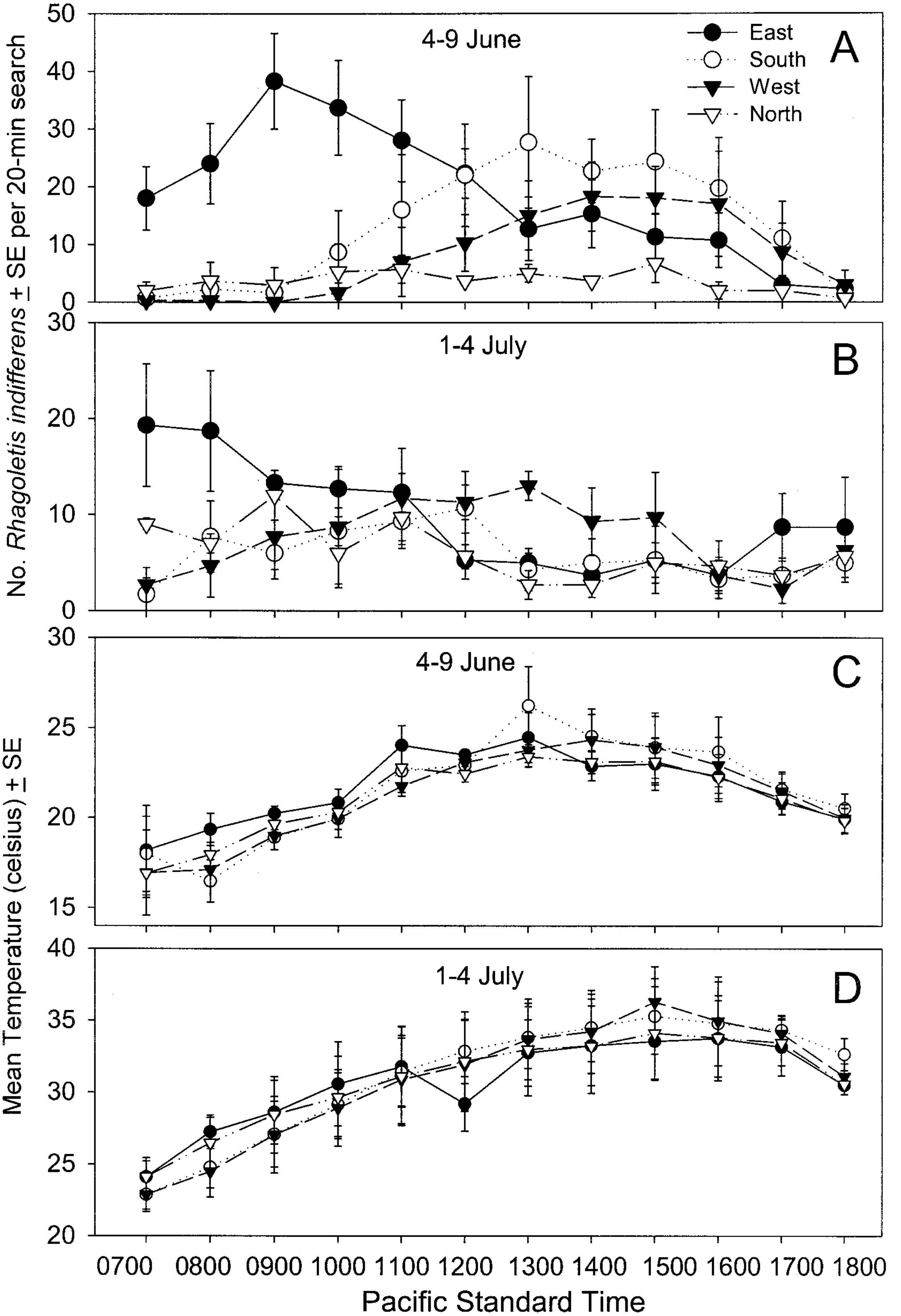

Fig. 3. Mean numbers ± SE of *R. indifferens* seen among tree quadrants on three sweet cherry trees during (A) 4–9 June and (B) 1–4 July and mean temperatures ± SE during (C) 4–9 June and (D) 1–4 July 2001 in Zillah and Yakima, WA.

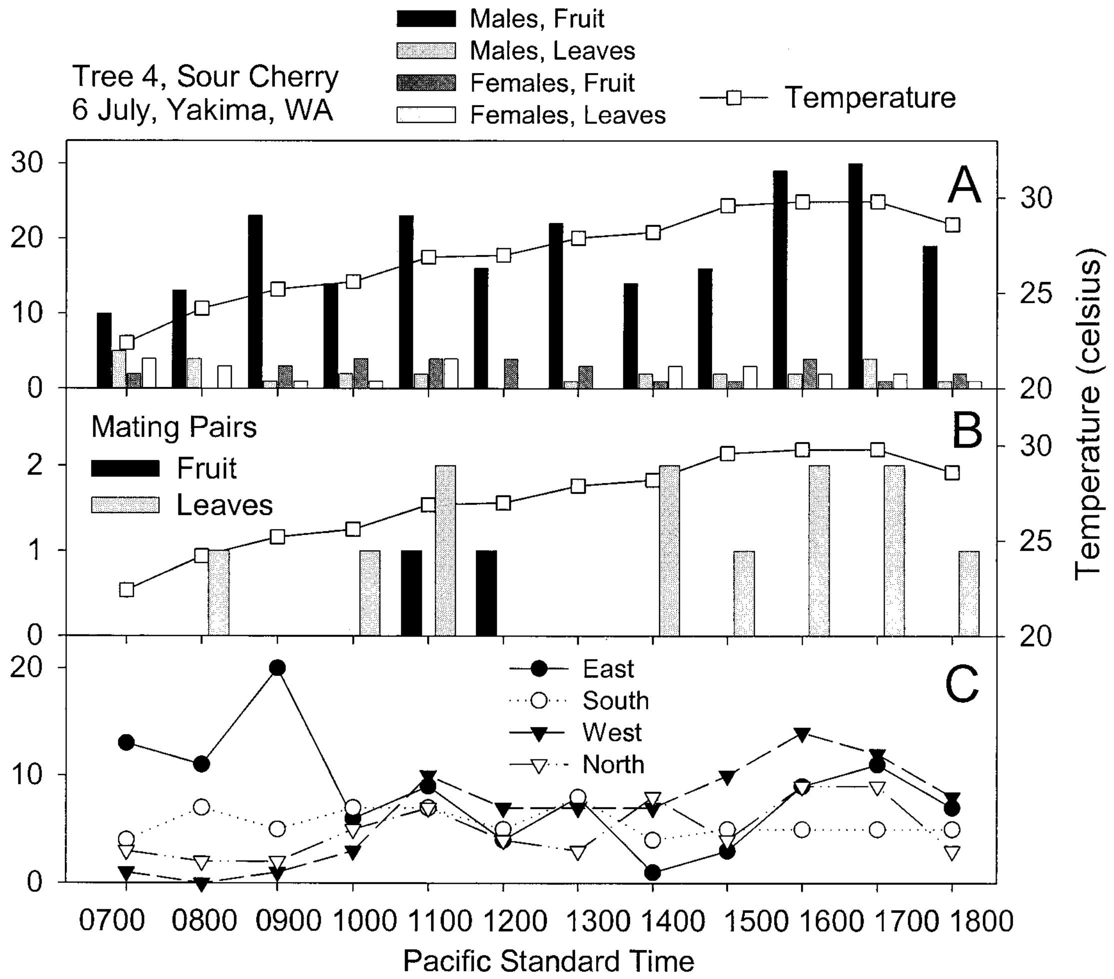

Fig. 4. Male and female *R. indifferens* activity on a sour cherry tree: (A) numbers on fruit and leaves, (B) numbers of mating pairs (20 min), and (C) numbers among tree quadrants (5 min each) over 12 h in Yakima, WA

seen in *R. pomonella* (Prokopy et al. 1972). As temperatures dropped to <20°C in the evening, male flies left the fruit again. However, the male flies did not move back onto leaves that were in view. Later in the season, when it was daylight and >35°C, most flies also disappeared from view. Unlike *R. fausta* (Prokopy 1976), *R. conversa* (Frías et al. 1984), and *R. zephyria* (Tracewski and Brunner 1987), which have been sighted on nonhost plants, no *R. indifferens* were seen on the sparse surrounding nonhost vegetation during these times. Where *R. indifferens* goes at nightfall and during periods of low and high temperatures is unknown. Presumably, flies moved vertically, as in *R. pomonella* (Prokopy et al. 1972, Prokopy and Papaj 2000), toward light that hit the treetops as the sun began to set. At extreme high temperatures, most flies may escape heat stress by moving to cooler parts of the tree or even to shady areas on the ground. Because flies reappear as soon as the temperatures drop, the flies probably do not leave the tree or fly far from it during periods of high heat. *R. zephyria* appears to have low and high temperature thresholds of 17 and 35°C (Tracewski and Brunner 1987) that are very similar to those of *R. indifferens.*

During the day, male *R. indifferens* visited fruit more and spent more time on fruit than leaves, which is the case with all male *Rhagoletis* spp. studied: *R. pomonella* (Prokopy et al. 1972), *R. fausta* (Prokopy 1976), *R. mendax* (Smith and Prokopy 1981), *R. cingulata* (Smith 1984), *R. conversa* (Frías et al. 1984), *R. cornivora* (Smith 1985a), *R. tabellaria* (Smith 1985b), and *R. zephyria* (Tracewski and Brunner 1987), and likely *R. cerasi* L. (Russ et al. 1973). Male *R. indifferens* wait on fruit for mating and engage in boxing behavior with other males to defend their territory (AliNiazee 1974). This behavior increased in the current study when densities of males were high (or when fruit densities were low), which was not consistent with laboratory results that showed that high male density reduced territoriality (AliNiazee 1974). There was no change in frequency of fruit use by males over the season, suggesting the preference for fruit was not affected to any large degree by the flies' age (except perhaps when flies are only a few days old), unlike in *R. zephyria,* in which males spent equal time on fruit and leaves early in the season but more time on fruit later (Tracewski and Brunner 1987).

Studies show most *Rhagoletis* females do not visit fruit and leaves equally, in sharp contrast with *R. indifferens* females. Although not all these studies used the same parameters as this study, most showed that female *Rhagoletis* at some time during the season made more visits or spent more time (or both) on fruit than on leaves. This was true of *R. pomonella* (more visits; Prokopy et al. 1972), *R. fausta* (more time; Prokopy 1976), *R. mendax* (more visits; Smith and Prokopy 1981), *R. cingulata* (both; Smith 1984), *R. cornivora* (both; Smith 1985a), and *R. zephyria* (both; Tracewski and Brunner 1987). However, *R. conversa* (Frías et al. 1984) and *R. tabellaria* (Smith 1985b) females visited both equally, with the latter also spending more time on leaves (although this was attributed to light fruit load on trees). The relatively high visitation of leaves by *R. indifferens* females may reflect the high nutrition found on leaves, causing females to seek them as a source of food. Alternatively, it may reflect the opposite. Cherry leaves may have only small quantities of nutrients on their surfaces, forcing the female flies to spend large amounts of time searching on many leaves.

There was no evidence that female *R. indifferens* visited leaves more often early in the season and fruit later, unlike female *R. fausta* (Prokopy 1976), *R. pomonella* (Prokopy 1977), and *R. zephyria* (Tracewski and Brunner 1987), which apparently switch from mostly seeking leaves (food sites) to fruit (egg-laying sites) as the flies mature over the season. Perhaps *R. indifferens* females are more dependent on nutrients on leaves than are other species and need to continually forage on leaves later in life to maximize egg production. Carbohydrates (leachates) (Hendrichs et al. 1993) and other unidentified substances on leaf surfaces may provide nutrition that is higher in quality than that found on surfaces of fruit. The fact that females spend a large amount of time on leaves throughout the season and may feed there suggests that management strategies could be targeted on leaves, perhaps by use of baits that adhere mostly to leaves and not to fruit.

The difference in male and female use of leaves and fruit may be explained if females feed more than males as with *R. mendax* (Smith and Prokopy 1981) and *R. cingulata* (Smith 1984). Females require protein and sugar to maximize egg development, whereas males require mostly sugar for spermatogenesis, at least in *R. pomonella* (Webster and Stoffolano 1978). Male *R. indifferens* perhaps do not feed on leaves as often as females because they need less protein and subsequently were sighted less on leaves. The lower numbers of female *R. indifferens* seen reflected the greater movement or higher foraging activities of females rather than a difference in the male:female ratio, which was 54:46 based on flies emerging under soil cages (Frick et al. 1954). This is consistent with findings in *R. pomonella* (Prokopy et al. 1972), *R. mendax* (Smith and Prokopy 1981), *R. conversa* (Frías et al. 1984), and *R. turpiniae* (Aluja et al. 2001), although in the first three species, the male bias was not as great as in *R. indifferens.*

There was no defined mating period during the day in *R. indifferens* as long as temperatures were 20–35°C, which is similar to *R. pomonella* (Prokopy et al. 1972) and *R. conversa* (Frías et al. 1984). Mating by *R. indifferens* was initiated on fruit, which has been observed before (AliNiazee 1974), but systematic searches for mating initiation on leaves had never been reported. Mating initiation on fruit was expected because males were found almost exclusively on fruit most of the day, presumably waiting for females. In this respect, *R. indifferens* seems different than *R. fausta* (Prokopy 1976) and *R. cingulata* (Smith 1984), in which all of the observed copulation attempts (albeit few) were initiated on leaves, but it is similar to *Rhagoletis completa* Cresson (Boyce 1934), *R. pomonella* (Prokopy et al. 1971), *R. conversa* (Frías et al. 1984), and *R. turpiniae* (Aluja et al. 2001). It seems likely, though, that *R. indifferens* would initiate mating on leaves earlier in the day (at ≈20°C), when more males were congregated on them, and females had not moved onto fruit.

Changes in daily and seasonal horizontal movement of *R. indifferens* within trees have been noted before (Frick et al. 1954), as they have been for *R. cerasi* (Prokopy 1969) and *R. pomonella* (Prokopy et al. 1972), with flies generally distributing themselves on the most sunlit parts of trees. Light intensity clearly had a positive effect on within-tree movement of *R. indifferens,* but later in the season at >35°C, it had a negative effect as flies avoided the sunny sides of trees. This explains the negative correlations between sightings and light intensity and temperature. This movement of *R. indifferens* among quadrants as affected by temperature may be a reason why fruit within trees can be uniformly infested over the season (Frick et al. 1954, Messina 1989). The movement also indicates that locations of traps within trees and time of day should affect detection and capture rates of *R. indifferens.*

The activities on sour cherry were essentially the same as on sweet cherry. Because the native host of *R. indifferens* is presumed to be the bitter cherry, *Prunus emarginata* Dougl. ex Eaton (Frick et al. 1954), it will be important to determine activity patterns on this host and compare them with patterns on cultivated cherries. The native cherry has small, narrow leaves and bright red fruit and exists either as a tall slender tree or a shrub (Lyons and Merilees 1995), major morphological characteristics that differentiate it from the cultivated cherries. Whether fly activity patterns and substrate use might have changed after the fly adapted to cultivated cherries needs to be examined.

In summary, the results show that *R. indifferens* presence and times spent on fruit and leaves were greatly altered by daily and seasonal changes in temperature, but they also suggest that at 20–35°C substrate-seeking behaviors of each sex do not change with time of day or season. Males of *R. indifferens* visited fruit more than leaves, like nine other *Rhagoletis* spp. that have been studied. Females visited fruit and leaves equally, like only two of these species, although use of different parameters among studies makes direct comparisons difficult. To further understand the ecology of *R. indifferens* and how it differs from that of other species, the effects of factors such as fruit load (Messina 1989), tree size, surrounding host vegetation, and tree density on fly activity patterns and inter-tree movement need to be examined experimentally.

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